

Geographic Variation in Flight Wing Development and Body Size of the Tule Beetle, *Tanystoma maculicolle* (Coleoptera: Carabidae)

JAMES K. LIEBHERR AND ANN E. HAJEK

Department of Entomology, Cornell University, Ithaca, New York 14853.

Abstract.—The tule beetle, *Tanystoma maculicolle* (Coleoptera: Carabidae), a common ground beetle in California, shows considerable geographic variability in flight wing development and body size. Flight wings may be fully developed or reduced to flap-like stubs. Ecologically marginal populations on the mainland exhibit high percentages of fully winged individuals, whereas populations from more mesic habitats and from the California Channel Islands are predominantly brachypterous. Populations with high percentages of macropterous individuals are restricted to ecologically marginal habitats, suggesting frequent extinction and recolonization in these areas.

On the mainland, body size increases clinally from south to north. Stepping-stone gene flow between mainland populations would facilitate this clinal variation. Body size of Channel Island populations varies erratically from south to north but is positively correlated with the floristic diversity of the islands.

The tule beetle, *Tanystoma maculicolle* (Dejean), is a common carabid beetle of mesic, open and woodland habitats in California, northern Baja California, and southern Oregon (Liebherr, 1985). In California, it occupies lowland habitats in the Central Valley which are hot and dry during the summer, along with more mesic, mid-elevational habitats in the foothills of the Coast Range and Sierra Nevada. Coast Range habitats receive more winter rain than Central Valley habitats, and the climate is moderated by a maritime influence. Sierra Nevada foothill habitats regularly receive winter rains and snow, as well as spring and summer runoff from snowfall at higher elevations. Tule beetle larvae develop during the winter, and most adults eclose from March to June (Liebherr, 1984). Thus, the occurrence of the larvae and pupae, the stages most susceptible to desiccation, is synchronized with the period of winter rains.

The tule beetle exhibits flight wing dimorphism across its distributional range (Liebherr, 1985). The macropterous morph possesses a well-developed flight apparatus; the metepisternum is elongate, and internal apodemes of the metanotum are evident. The flight wings range from 1.3 to 1.5 × the length of the elytra. The brachypterous morph has a much shorter metepisternum, the internal apodemes of the metanotum are much reduced, and the flight wings are short scale-like flaps that extend only to the base of the abdomen.

This paper first describes the geographic variation in flight wing configuration in this species, and investigates the relationship between habitat stability and flight wing development. Secondly, the patterns of body size variation on the

mainland are compared with those on the California Channel Islands. Comparison of the isolated populations on islands with ecologically marginal populations on the mainland suggests fundamental differences in selective regimes acting on the two types of populations.

MATERIALS AND METHODS

Our evaluation of the geographic distribution of macroptery and brachyptery in *T. maculicolle* is based on museum material used in a taxonomic revision of the genus *Tanystoma* (Liebherr, 1985). Presence or absence of fully developed flight wings can be observed through the semi-hyaline areas of the maculate elytra, or by lifting the apex of an elytron. To determine the geographic distribution of fully flighted forms, we excluded specimens possibly collected at light. Although this results in fewer samples, it eliminates any bias toward flighted forms. Data for males and females were recorded separately for flight wing dimorphic populations. Because no difference in flight wing configuration was attributable to sex, the sexes were pooled in all samples. Specimens collected on different dates at particular localities were also pooled because no temporal variation was observed in the material at hand.

We used elytral length as a measure of body size. Elytral length is highly correlated with overall body size (Liebherr, 1986), and measurement of the elytra rather than overall body length eliminates error due to the posture of pinned specimens. Elytra were measured from the tip of the mesoscutellum to the elytral apex. Specimens were held horizontally in a rotatable specimen holder, and measured using a calibrated ocular grid. On average, females are larger than males, so the sexes were analyzed separately. Seven mainland localities were compared to 7 samples from the Channel Islands. Twenty individuals of each sex were measured for most localities; the smaller sample sizes from some localities are due to a shortage of material. Results are portrayed using Dice-Leraas diagrams with the modifications suggested by Simpson et al. (1960).

As body size of the beetles varies among the California Channel Islands, biological attributes of the islands were investigated to determine whether they are correlated with the pattern of body size variation. Floristic diversity, measured by the number of plant associations present on each island (Philbrick and Haller, 1977), was used as an independent variable upon which elytral length was regressed. Floristic associations that occur in habitats unsuitable for *T. maculicolle* were excluded from the analysis; this limited the associations tallied to island chaparral, valley and foothill grassland, southern coastal oak woodland, island woodland, southern riparian woodland, Bishop pine forest, Torrey pine forest, and coastal marsh (Philbrick and Haller, 1977).

RESULTS

The proportion of macropterous individuals ranges from 1.0 (Warner Springs, Brentwood) to 0 (San Jacinto Mtns., several Channel Islands, Three Rivers, Tiburon, and Oroville) (Appendix 1). The pattern of flight wing variation is a mosaic, with abrupt frequency changes occurring over short distances within the species' range (Fig. 1). For example, the macropterous Warner Springs sample ($n = 17$) was taken at most 70 km away from the totally brachypterous San Jacinto Mountains sample ($n = 13$) (different at $P < 0.001$, chi-squared = 30.3, d.f. = 1). The

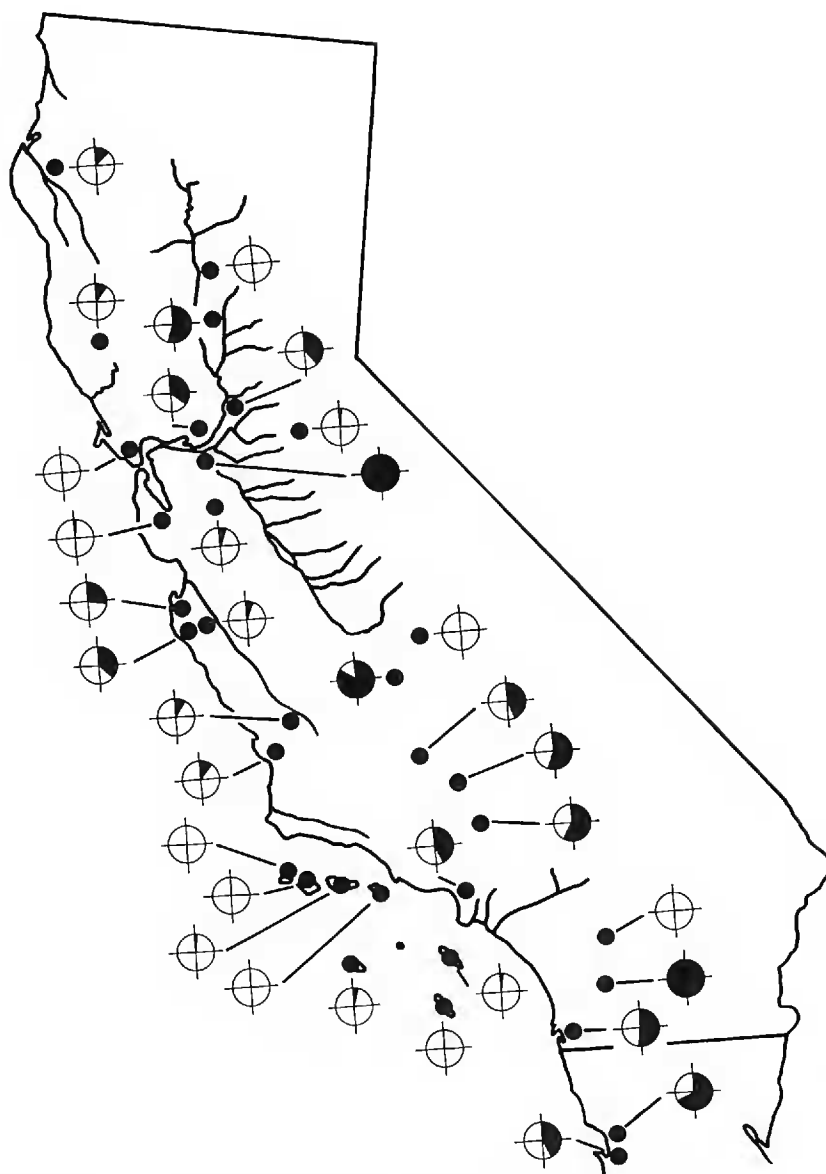


Figure 1. Percentage of macropterous (solid) and brachypterous (open) *Tanystoma maculicolle* from 34 localities in California and northern Baja California (see Appendix 1 for numbers of specimens in each sample).

Tipton sample ($n = 8$) has 7 individuals winged, whereas the Three Rivers sample ($n = 11$) from 55 km away is 100% brachypterous (different at $P < 0.001$, chi-squared = 15.3, d.f. = 1).

In general, populations from the floor of the Central Valley, Los Angeles, and the southernmost portion of the range exhibit the highest fraction of fully winged individuals. Populations along the coast are more variable. The Carmel and Big Sur samples contain 27% and 37% macropterous beetles, whereas other coastal samples (San Luis Obispo, Paso Robles, Paraiso Springs, Stanford, Tiburon, Hopland, Humboldt Co.) range from 0 to 13% macropterous. The few samples available from higher elevations (e.g., Three Rivers [250 m], West Point [650 m], and San Jacinto Mtns.) exhibit a high proportion of brachypterous beetles.

Almost all beetles on the Channel Islands are brachypterous. Sample sizes are quite large for most of the islands, and only the Sta. Catalina, San Nicolas, and Sta. Cruz island samples contain any macropterous individuals. The only fully winged beetle from Sta. Catalina Isl. is teneral, indicating this specimen actually eclosed on the island. San Nicolas Isl., the most isolated of the islands and farthest from the mainland, has 5% macropterous individuals. The closest mainland samples to compare with the Channel Island populations are San Diego and Los Angeles. These samples contain 52 and 43% macropterous individuals, respectively.

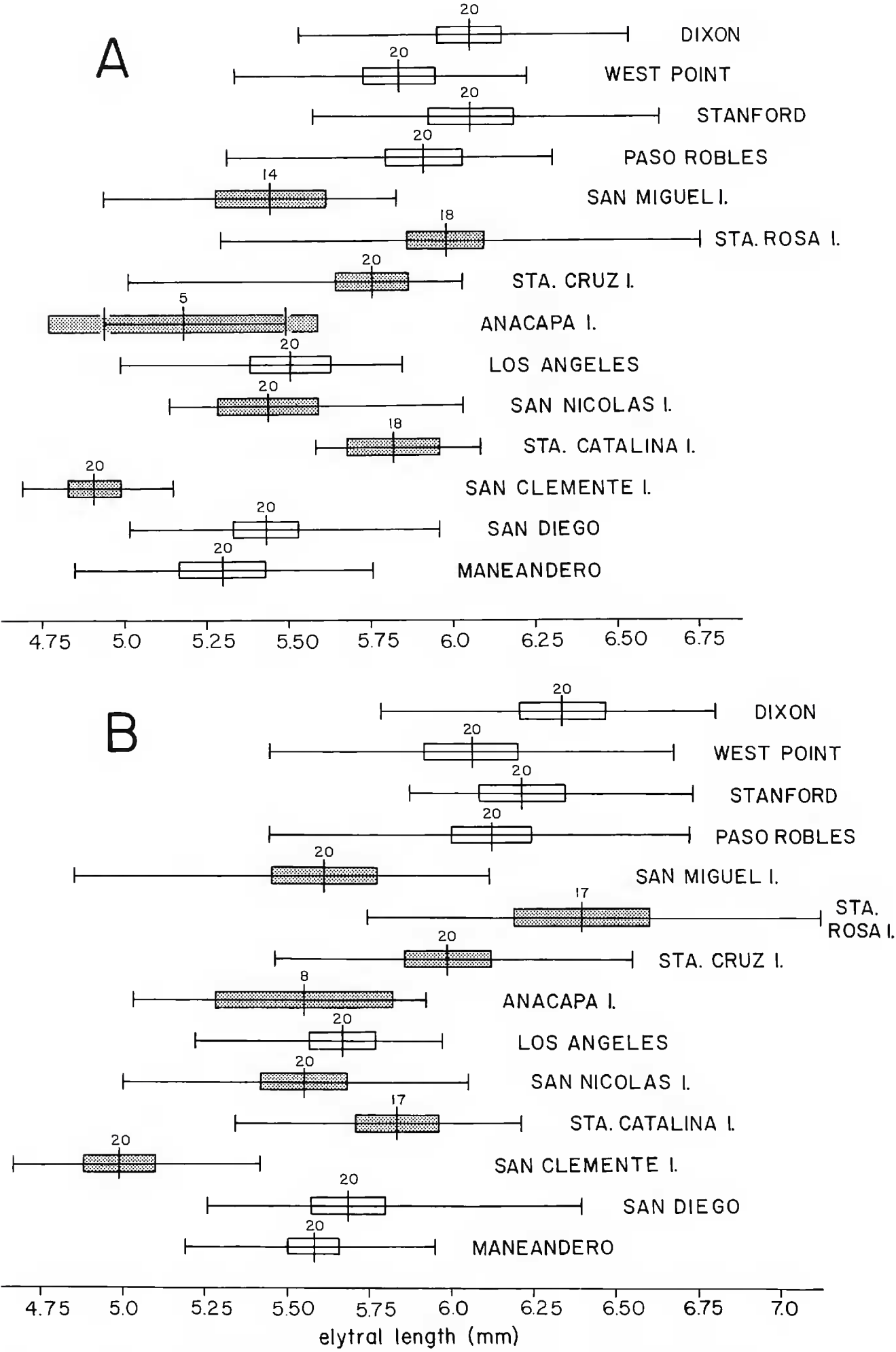


Figure 2. Dice-Leraas diagram showing elytral length for 7 California mainland (open) and 7 Channel Island (shaded) populations. Range shown as long line; box represents 95% confidence interval about mean ($\bar{x} \pm t_{0.5, n-1} \times s/n^{1/2}$); number above mean is sample size. Samples are ordered by latitude, from south to north. A) Males. B) Females.

Table 1. Mean elytral length for males and females of *Tanystoma maculicolle* from the Channel Islands, and the number of plant associations on each island suitable for habitation by the species.

Island	$\bar{x}$ (♂♂)	$\bar{x}$ (♀♀)	# plant associations
San Clemente	4.91	4.99	3
Sta. Catalina	5.82	5.83	6
San Nicolas	5.44	5.55	2
Anacapa	5.18	5.55	1
Sta. Cruz	5.76	5.98	7
Sta. Rosa	5.98	6.39	8
San Miguel	5.45	5.61	1

Average elytral length varies from 4.92 mm (San Clemente Isl.) to 6.06 mm (Dixon and Stanford) for male beetles, and 4.98 mm (San Clemente Isl.) to 6.38 mm (Sta. Rosa Isl.) for females (Fig. 2). Mainland populations of both males and females exhibit a relatively smooth increase in body size from south to north. Maneadero, Baja California averages the smallest of the mainland samples, San Diego and Los Angeles average somewhat larger, and the 4 northernmost samples are the largest of the mainland samples. Within sample variability is similar in all 7 mainland samples.

The Channel Island samples exhibit a very erratic pattern of body size variation from south to north (Fig. 2). San Clemente Isl. beetles are significantly smaller than those of any other island or mainland population, except the small sample of beetles from Anacapa Isl. The Sta. Catalina, Sta. Cruz, and Sta. Rosa samples have the largest beetles among the island populations. Several beetles from Sta. Rosa Isl. are actually larger than any of the other mainland or island specimens.

The variation in body size is much greater among the island populations than among populations from the larger mainland area. When differences between the geographically adjacent localities in Figure 2 are averaged, for males the change in elytral length per km map distance is 0.039 mm/km in the island populations versus 0.00087 mm/km for the mainland populations ($t = 85.7$, d.f. = 12, $P \ll 0.01$). For female beetles, adjacent island populations differ in elytral length by an average of 0.046 mm/km, whereas mainland populations change by 0.00095 mm/km ($t = 58.2$, d.f. = 12, $P \ll 0.01$).

For our 7 Channel Island samples, average elytral length is positively correlated with the number of plant associations available to *T. maculicolle* on each island (Table 1, Fig. 3). For males, the regression of elytral length on number of plant associations produces the equation $y = 0.099x + 5.11$, with a slope significantly different from zero ($t = 2.73$, d.f. = 6, $P < 0.05$). The regression accounts for nearly 60% of the variation in the data set. Female beetles are also larger on floristically more diverse islands ($y = 0.108x + 5.27$; $t = 2.39$, d.f. = 6, $P < 0.05$). Over 53% of sample variation can be accounted for by this regression. In both sexes, beetles from San Clemente Island are much smaller than expected based on the regression ($P < 0.001$ for both sexes).

A very limited sample of male beetles from Guadalupe Isl., Baja California Norte, has an average elytral length of 5.33 mm ($n = 5$, range 5.11–5.73 mm). The body size on Guadalupe Isl. does not differ significantly from that at Maneadero, the nearest mainland locality.

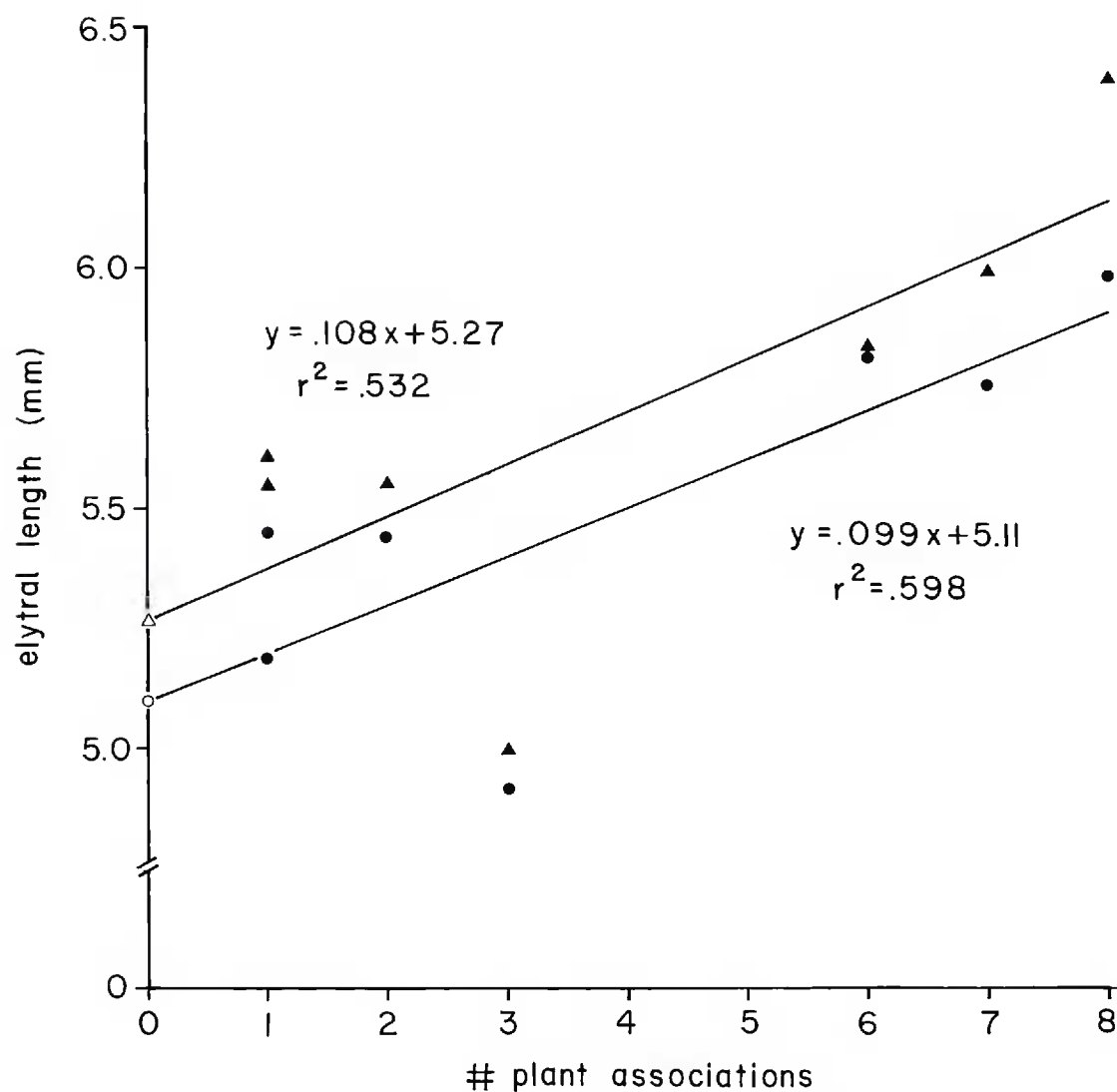


Figure 3. Regression of average elytral length (mm) on number of plant associations suitable for *Tanystoma maculicolle* males (●) and females (▲) on the California Channel Islands (see Table 1).

DISCUSSION

Wing polymorphism.—A dispersal polymorphism can be interpreted as an evolutionary response that permits a species to utilize a mosaic of stable and temporary habitats. Darlington (1943) reported that brachypterous carabids are concentrated in mountains and mountainous islands, apparently because flight is not required in these limited habitats. Brachyptery is not limited to mountain inhabiting populations of *Notiophilus biguttatus* (F.) in Bohemia. Lowland populations may also contain up to 30% brachypterous individuals (Honěk, 1981), demonstrating that higher altitudes are not the only habitats in which brachyptery can occur.

Based on data from carabid species that had colonized areas glaciated during the last glaciation, Lindroth (1969, 1979) hypothesized that regions with high percentages of brachypterous individuals had served as glacial refugia. He argued that these more stable areas maintained wingless stocks, whereas colonization of newly available habitats proceeded by macropterous propagules. Such a relationship between habitat age and brachyptery has also been reported for 3 species of capniid Plecoptera in Alberta (Donald and Patriquin, 1983). Vepsäläinen (1978) adds that isolation is frequently characteristic of brachypterous populations in genetically determined polymorphic species. Among Gerridae (Hemiptera), isolated populations receive few macropterous colonists, enhancing the trend toward brachyptery.

Southwood (1962) extended Lindroth's historically based hypothesis, general-

izing that dispersal from habitats of origin is the means by which species colonize changing or temporary habitats. This hypothesis has been corroborated by numerous studies of insects (Greenslade and Southwood, 1962; Den Boer, 1970, 1971, 1979; Denno, 1976, 1979; Vepsäläinen, 1978). Maintaining a fraction of vagile colonizing individuals in a population assures the ability to colonize nearby habitats where extinction has occurred.

For *Tanystoma maculicolle*, an hypothesis of relatively frequent extinction and refounding of populations due to environmental fluctuations in marginal habitats is consistent with our findings. Localities in the Central Valley, and lower elevational sites in the southern part of the range have the highest percentage of winged individuals. These localities are the most unpredictable in terms of habitat suitability for these winter and spring breeding beetles; i.e., winter rainfall is the least and its occurrence sporadic. By comparison, the more mesic mainland habitats which receive more winter rain, and the geographically isolated Channel Island populations have higher percentages of brachypterous individuals.

That the Channel Islands were never connected to the mainland during Pleistocene sea-level fluctuations is now well established (Junger and Johnson, 1980). We conclude therefore that the islands were colonized by *T. maculicolle* from the adjacent mainland. The relatively high percentage of macropterous individuals in Los Angeles and San Diego suggests that the islands were colonized by winged propagules, and that selection pressure is acting against macroptery on the islands. Although colonization of the islands by macropterous individuals is most likely, brachypterous beetles may also have colonized as suggested by Ås (1984) for carabids colonizing islands in the Baltic Sea.

Several bases for selective advantage of winglessness on islands have been proposed. The notion that winged individuals may be blown away from suitable habitats or face more environmental hazards on islands has been attributed to Darwin (1859), and recently supported by Den Boer et al. (1980) and Bengtson and Eriksted (1984). Several of the Channel Islands (San Clemente, Sta. Catalina, Sta. Cruz, Sta. Rosa) are large enough to support a number of localized populations of *T. maculicolle*. These local populations occur in a variety of woodland and grassland habitats. In this case it is apparent that flight activity would not necessarily result in movement to unsuitable habitats, or off-island dispersal. We feel an hypothesis in which the frequency of macropters is reduced solely due to dispersal cannot completely explain the near total brachyptery on the Channel Islands.

Other hypotheses for the evolution of brachyptery stem from Darlington's (1943) suggestion that brachypterous individuals are favored when dispersal is not required for maintenance of the population. Among gerrids (Vepsäläinen, 1978; Zera, 1984) and aphids (Wratten, 1977), flightless morphs are more fecund and frequently develop faster than flighted morphs. Such an occurrence would give a selective advantage to brachypterous individuals of *T. maculicolle* if density-dependent mortality acted on the populations. One such mortality factor operating within populations could be cannibalism. The larval stages of *T. maculicolle* are voracious predators, and often cannibalistic when reared together (Liebherr, 1984, unpubl. data). *T. maculicolle* is a very common species, often occurring in dense populations. If the larvae of wingless individuals develop faster, cannibalism would exert strong selective pressure to reduce the frequency of slower

developing macropters in dense populations. A combination of intrasite advantage for brachypters, and lack of winged immigrants due to isolation would be sufficient to explain the absence of macropters on the Channel Islands.

Body size.—Body size in mainland populations of *T. maculicolle* increases clinally from the southern to northern limits of the distributional range (Fig. 2). The gradual change in body size is consistent with an isolation by distance model of differentiation (Wright, 1943) influenced by uniformly changing selection pressure.

In *Eusattus muricatus* LeConte, a sand dune inhabiting tenebrionid beetle, specimens from southern California are larger than specimens from northern California (Doyen and Rogers, 1984). A longer period for larval development in the southern portion of the range is believed to be the determinant for larger body size. Southern populations of this univoltine species can develop year round, whereas northern populations must cease activity during winter.

The tule beetle breeds during the rainy California winter and teneral adults are present from March to June (Liebherr, 1984). Large body size in northern populations is associated with the longer rainy season there. Southern populations have a much shorter period for larval development because of the shorter rainy season. The converse clines in body size variation observed in *E. muricatus* and *T. maculicolle* can both be related to the length of the larval developmental period. Differences in habitat preference and phenology appear to govern the difference in body size clines between these species.

The pattern of body size variation among all of the Channel Islands is a mosaic (Fig. 2), but is positively correlated with floristic diversity (Table 1, Fig. 3). The variety of plant associations on an island can be considered an indication of the general suitability of an island for larval development. It is not known whether floral diversity is indicative of general moisture conditions, the quality or quantity of prey, or other factors influencing the size of adult *T. maculicolle*.

The 4 northern Channel Islands (San Miguel, Anacapa, Sta. Rosa, and Sta. Cruz) were united in a superisland, Santarosae, during periods of maximum sea-level lowering in the Pleistocene (Wenner and Johnson, 1980). Yet, distinct differences in body size exist among tule beetle populations on these islands today. The San Miguel and Anacapa populations have significantly smaller beetles than those on Sta. Cruz or Sta. Rosa. The intense stripping of vegetation on San Miguel Isl. (Johnson, 1980) has left only valley and foothill grassland (Philbrick and Haller, 1977) as habitats suitable for *T. maculicolle*. Due to its small size, Anacapa Isl. also has only grassland for *T. maculicolle* to inhabit. The Sta. Rosa and Sta. Cruz islands have a variety of chaparral, and oak and pine woodlands that are suitable for tule beetle populations. Among these 4 islands, the divergence in body size has occurred since the fragmentation of Santarosae. Whether differential selection pressures have resulted in genetic change among the island populations remains to be studied.

CONCLUSIONS

Tanystoma maculicolle populations that are isolated on islands or in ecologically marginal areas on the mainland possess fundamentally different characteristics. Island populations are predominantly brachypterous, with this reduced vagility suggesting very limited among-island dispersal. Island populations are

long-lived enough for substantial among-island divergence in body size to have arisen. In contrast, marginal mainland populations possess mostly winged individuals, and appear to be in genetic contact with adjacent populations based on clinal variation in body size. Population extinction is judged to be a relatively common occurrence on the mainland, based on the low frequency of brachypterous individuals in many of these populations.

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APPENDIX 1

Sample localities and numbers of brachypterous (B) and macropterous (M) individuals used in analysis of flight wing variation.

MEX: B.C. Norte, Guadalupe Isl. (4B, 1M); MEX: B.C. Norte, Maneadero (14B, 10M); MEX: B.C. Norte, Ensenada (5B, 11M); CA: San Diego Co., San Diego (14B, 15M); CA: S.D. Co., Warner Sprs. (0B, 17M); CA: Riverside Co., San Jacinto Mtns. (13B, 0M); CA: L.A. Co., Los Angeles (50B, 38M); CA: L.A. Co., Antelope (3B, 5M); CA: L.A. Co., San Clemente Isl. (168B, 0M); CA: L.A. Co., Sta. Catalina Isl. (35B, 1M); CA: Ventura Co., San Nicolas Isl. (113B, 6M); CA: Sta. Barbara Co., Anacapa Isl. (13B, 0M); CA: Sta. Barb. Co., Sta. Cruz Isl. (93B, 1M); CA: Sta. Barb. Co., Sta. Rosa Isl. (35B, 0M); CA: Sta. Barb. Co., San Miguel Isl. (46B, 0M); CA: Kern Co., Tehachapi Mtns. (4B, 5M); CA: Kern Co., Bakersfield (10B, 7M); CA: S.L.O. Co., San Luis Obispo (15B, 2M); CA: S.L.O. Co., Paso Robles (26B, 3M); CA: Tulare Co., Tipton (1B, 7M); CA: Tulare Co., Three Rivers (11B, 0M); CA: Monterey Co., Big Sur (5B, 3M); CA: Mont. Co., Paraiso Spgs. (27B, 2M); CA: Mont. Co., Carmel (8B, 3M); CA: Sta. Clara Co., Stanford (62B, 1M); CA: Alameda Co., Arroyo Mocho (37B, 3M); CA: Marin Co., Tiburon (19B, 0M); CA: Contra Costa Co., Brentwood (0B, 13M); CA: Solano Co., Dixon (33B, 19M); CA: Calaveras Co., West Point (52B, 1M); CA: Sac'to. Co., Sacramento (11B, 7M); CA: Yuba Co., Yuba City (4B, 5M); CA: Butte Co., Oroville (8B, 0M); CA: Mendocino Co., Hopland (9B, 1M); CA: Humboldt Co. (pooled localities) (7B, 1M); OR: (pooled localities) (9B, 2M).